

Non-lethal effect of the invasive predator *Bythotrephes longimanus* on *Daphnia mendotae*

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SUMMARY

1. We evaluated the antipredator behaviour of *Daphnia mendotae* to the invasive invertebrate predator, *Bythotrephes longimanus*, and the consequent effect of the predator on prey growth rate (referred to as a non-lethal effect of the predator).
2. In a laboratory experiment, *Daphnia* in the absence of *Bythotrephes* kairomones remained in the top, warmer regions of experimental columns, whereas in the presence of *Bythotrephes* kairomones, *Daphnia* migrated vertically, occupying a middle region by night and a low, cold region during the day. Over a 4-day experiment, the vertical migration induced by *Bythotrephes* caused a 36% reduction in the somatic growth rate of *Daphnia*, a level that is sufficient to have an effect on prey population growth rate.
3. A second laboratory experiment indicated that concentrations of *Bythotrephes* kairomones in water taken directly from the field (Lake Michigan) were high enough to induce behavioural shifts that led to these large reductions in somatic growth rate.
4. Our results identify a means by which *Bythotrephes* has substantial effects on native prey populations other than through direct consumption.

Keywords: *Bythotrephes*, *Daphnia*, diel vertical migration, non-lethal effects, trait-mediated interactions

Introduction

Understanding the impact of invasive species is one of the most important challenges facing biologists today (Mack *et al.*, 2000; Byers *et al.*, 2002; Hochberg & Gotelli, 2005). One clear effect of invasive species is predation on native prey, although potential non-lethal effects are less well understood. Non-lethal effects occur when prey respond to predators by a modification of their phenotype (e.g. behaviour, morphology and life-history) that may reduce predation risk (Lima, 1998). In theory, this phenotypic response increases fitness but, due to tradeoffs, there are costs, often in the form of reduced growth and fecundity (reviewed in Harvell, 1990). Empirical

(Lima, 1998; Werner & Peacor, 2003; Schmitz, Krivan & Ovadia, 2004) and theoretical studies (Abrams, 1982; Ives & Dobson, 1987; Abrams, 1993; Bolker *et al.*, 2003; Peacor & Werner, 2004) indicate that such non-lethal effects can be strong relative to direct consumption. Invasive predators have been shown to have non-lethal effects on native prey through induced phenotypic changes in several systems, including streams (McIntosh & Townsend, 1994), ponds (Shave, Townsend & Cowl, 1994; Pearl *et al.*, 2003) and terrestrial communities (Wilder & Rypstra, 2004). Thus, whereas it is important to understand the non-lethal effect of invasive predators to assess their impacts fully, our present view is derived from a limited number of systems.

Here, we examine non-lethal effects of an invasive predator, *Bythotrephes longimanus* (Leydig), on zooplankton prey in the pelagic zone of Lake Michigan through a well-known antipredator behaviour, vertical migration. *Bythotrephes* is an invasive

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predatory cladoceran that studies suggest has had an impact on the pelagic ecosystem of the Laurentian Great Lakes (Lehman & Caceres, 1993; Vanderploeg *et al.*, 2002; Barbiero & Tuchman, 2004) and smaller surrounding lakes (Yan *et al.*, 2001; Boudreau & Yan, 2003). In particular, since its introduction in the early 1980s, *Bythotrephes* has been described as a main factor driving community dynamics in Lake Michigan (Makarewicz *et al.*, 1995). Although research on the effects of *Bythotrephes* on its zooplankton prey has focused primarily on direct consumption, field observations in Lake Michigan indicate that *Bythotrephes* may induce downward migration of zooplankton prey (Lehman & Caceres, 1993; K.L. Pangle, unpublished data), which could affect prey growth rate. However, alternative processes could be responsible for the changes in zooplankton vertical distribution including: (1) another factor that is correlated with *Bythotrephes* density; (2) greater *Bythotrephes* predation of the entire prey population near the surface; (3) seasonal shifts in clones within a prey species that exhibit different behaviour; or (4) an indirect effect from *Bythotrephes* affecting some other environmental condition, such as attracting fish.

We used an experimental approach to examine if *Bythotrephes* changed the vertical distribution of *Daphnia mendotae* (Birge), and any non-lethal effect on growth rate caused by such a behavioural modification. *Daphnia mendotae* is an important food for *Bythotrephes* (Lehman, Bilkovic & Sullivan, 1997; Schulz & Yurista, 1999), and *Daphnia* is a model organism for the study of predator-induced tactics (Lass & Spaak, 2003). *Daphnia mendotae* has also been shown to respond to *Bythotrephes* kairomones (i.e. water-borne chemicals produced by the predator) by growing larger helmets (Bungartz & Branstrator, 2003). In the laboratory, we exposed *D. mendotae* to *Bythotrephes* kairomone over a 4-day period. We hypothesised that *D. mendotae* would respond by migrating downward, particularly during the day, because *Bythotrephes* is a visual predator (Muirhead & Sprules, 2003) that inhabits the epi- and metalimnetic portions of the water column in Lake Michigan (Lehman & Caceres, 1993; K.L. Pangle, unpublished data). Furthermore, we hypothesised that vertical migration into deeper, colder water would incur a cost to growth. A second laboratory experiment was conducted to link our laboratory results with the concentrations of *Bythotrephes* kairomones in water collected from Lake Michigan.

Methods

We measured the effect of *Bythotrephes* kairomones on the behaviour and growth rate of *D. mendotae* in experimental cylinders with a thermal gradient spanning a similar temperature range as that found in Lake Michigan. Experiment 1 was conducted to examine the effects of *Bythotrephes* kairomones on the vertical distribution of *Daphnia* and on individual (i.e. somatic) growth. Experiment 2 compared the response of *Daphnia* to lake water collected from regions with and without *Bythotrephes* and to a range of *Bythotrephes* kairomone concentrations prepared in the laboratory.

The experimental system followed that of Loose & Dawidowicz (1994). During the experiments, the vertical position of *Daphnia* was measured in 80-cm tall, 19-mm diameter, clear acrylic cylinders that were filled with experimental water and submerged vertically in a transparent, 300-L aquarium. The aquarium acted as a thermally stratified water bath, with water temperatures regulated to 23 °C at the surface and 12 °C at the bottom, using an external chiller unit. The cylinders were illuminated by diffused light from directly above using four, 50 W halogen bulbs. Light conditions followed a 14 h light : 10 h dark regime centred at 12 : 00, with a photon flux density of 20.0 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at the top of the cylinder and 4.0 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at the bottom during midday. During the transitions from day to night or *vice versa*, light intensity was gradually increased or decreased over a 2-h period. Water was pumped into each cylinder using two 24-channel peristaltic pumps via individual 0.38 mm-diameter tygon tubes at a rate of 13.3 mL h⁻¹, creating a 12-h residence time for the water in each cylinder. Given this rate of water flow, the supply rate of resources was approximately 20 times greater than the expected maximum clearance rate of the *Daphnia* (0.6 mL h⁻¹ individual⁻¹; Lurling, 2001), and therefore any effects of *Daphnia* grazing of food were negligible.

In both experiments, we measured the vertical position of *Daphnia* by recording the depth interval occupied. Cylinders were demarcated into 10 intervals total, with two 5-cm intervals at the top, two 5-cm intervals at the bottom, and six 10-cm intervals in the middle. We used mean depth (cm) and the percentage of individuals in the upper and lower 5-cm extremes of the cylinder as measures of the vertical position of

Daphnia. 'Depth' was defined as the midpoint of the depth interval in which *Daphnia* were observed.

Daphnia mendotae was collected from Lake Michigan on 12 July 2004 using a zooplankton net with a closed bucket towed vertically through the entire water column. Collections occurred approximately 8 km offshore of Muskegon, Michigan, an area inhabited by *Bythotrephes* (K.L. Pangle, personal observation). The *Daphnia* were then maintained in 4-L vessels in aged Lake Michigan water at 20 °C with a 14 h light : 10 h dark light regime. They were fed *Nanochloropsis limnetica* (Hibberd) (SAG 18.99, University of Gottingen, Sag, Germany) at approximately 6 mg C L⁻¹. The *Bythotrephes* used in the experiments were collected in a similar fashion at the same location on 6 August and 7 September 2004, and maintained individually in 50-mL glass containers at the same temperature and light conditions as *Daphnia* and were fed 5 *Daphnia* day⁻¹.

Experiment 1 was conducted from 9 to 13 August 2004. During the experiment, *Daphnia* were kept in either a control water treatment or in a *Bythotrephes* water treatment. Control water was lake water passed through a 0.45-µm filter and aged at room temperature over a 14-day period, a sufficient duration for breakdown of pre-existing kairomones (Loose, von Elert & Dawidowicz, 1993). To create *Bythotrephes* water (density, 5 *Bythotrephes* L⁻¹), individual *Bythotrephes* were incubated in control water in separate 200-mL containers for a 24-h period. Fresh *Bythotrephes* water was created on seven separate occasions over the course of the experiment, so it could be replaced every 12 h. *Bythotrephes* were not fed during the incubation period. The control water used in the experiment was maintained under similar condition with no *Bythotrephes* added. Two hours prior to the experiment, *Bythotrephes* were removed from each container, and *Bythotrephes* water and control water passed through a 64-µm filter to remove any debris. For food, *Nanochloropsis* was added to all experimental water (6 mg L⁻¹). Some of the experimental water was used to fill respective cylinders, while the remainder was transferred to reservoirs that supplied the peristaltic pump system. Treatments were assigned to cylinders using a randomised block design; each of the two treatments was represented in 10 spatial blocks, with each consecutive two cylinders representing a block (20 cylinders aligned side by side in total).

Daphnia used in the experiment were neonates, born 4–5 days beforehand. This ensured that the organisms were initially of uniform size and developmental state, and the young age reduced the chance of *Daphnia* producing offspring during the experiment. One *Daphnia* was transferred into each cylinder and allowed to acclimate to experimental conditions for 1 h before observations began. An additional 20 *Daphnia* were picked haphazardly and measured to estimate the initial size.

The experiment started at noon and continued for 4 days. The vertical position of each *Daphnia* was determined every 12 h (nine observations in total), coinciding with noon and midnight. At the end of the experiment, the *Daphnia* were removed from each cylinder and preserved in a sugar-formalin solution. Standard body length of each *Daphnia* was later measured under 40× magnification using a drawing tube and digitiser (Roff & Hopcroft, 1986). Standard body length was converted to dry weight using a standard equation (Dorazio, Bowers & Lehman, 1987) to determine the absolute weight gain over the duration of the experiment. In addition, specific growth rate (SGR) in mass was calculated as

$$\text{SGR} = \frac{\ln(W_f) - \ln(W_i)}{d},$$

where W_f is final dry weight (µg), W_i the initial dry weight (µg), and d the duration of the experiment (days).

Experiment 2 was conducted on 8 September 2004. *Daphnia* were kept in one of six water treatments including: control water; three concentrations of laboratory prepared *Bythotrephes* water, low, medium, and high; lake water not inhabited by *Bythotrephes*; and lake water inhabited by *Bythotrephes*. This design allowed us both to compare the concentrations of kairomones in Lake Michigan with those created in the laboratory, and also to evaluate the effect of predator density on vertical migration. Lake water was collected from depths of the water column where *Bythotrephes* is known to be most and least abundant (K.L. Pangle, unpublished data). Specifically, 1000 L of lake water was pumped from 1 and 20-m depths where *Bythotrephes* was absent (no *Bythotrephes* were found) and present (approximately 0.010 *Bythotrephes* L⁻¹), respectively, at 16:00 on 7 September 2004 at the same site where experimental *Daphnia* and

Bythotrephes were collected. At the time of sampling, the Lake Michigan water column was stratified, with a thermocline at approximately 20 m. During the period between water collection and the start of the experiment, lake water was maintained in the dark at 4 °C to reduce kairomone breakdown. The control water, and water prepared in the laboratory with a high density of *Bythotrephes* (5 L⁻¹), was made in a similar fashion as experiment 1. Laboratory prepared water with low and medium *Bythotrephes* density (0.05 and 0.5 L⁻¹, respectively) was made through serial dilutions of the 'high density' prepared water. For food, *Nanochloropsis* (6 mg L⁻¹) was added to all experimental water. In contrast to experiment 1, six replicate cylinders were designated to each treatment, and each cylinder received six *D. mendotae*. Treatments were assigned to cylinders using a randomised block design; each of the six treatments was represented in six spatial blocks, with each consecutive six cylinders representing a block (36 cylinders aligned side by side in total). Five observations were taken from 10:00 to 14:00 in 1-h intervals. All other experimental conditions were as described in experiment 1.

In experiment 1, a repeated-measures analysis of variance (ANOVA) was used to evaluate the effect of *Bythotrephes* kairomone on *Daphnia* vertical position during the day and night over the duration of the experiment. In addition, the secondary effects of *Bythotrephes* kairomone on absolute weight gain and specific growth rate of *Daphnia* were evaluated using a

blocked one-way ANOVA. In experiment 2, the behavioural responses were averaged over all *Daphnia* within each cylinder over the duration of the experiment. The behavioural response of *Daphnia* to each treatment was analysed using a blocked one-way ANOVA. When significant differences among treatments were detected, a Tukey pairwise comparison was used to separate the means. All percentage data was arc-sin transformed prior to analysis (Zar, 1999).

Results

Daphnia responded to *Bythotrephes* kairomones by migrating downwards into cooler water. In experiment 1, *Daphnia* remained high in the experimental columns by both day and night in the absence of *Bythotrephes* kairomones but, when in the *Bythotrephes* water, the *Daphnia* were significantly deeper ($F_{1,157} = 91.06$; $P < 0.01$) particularly during the day [significant interaction between kairomones and photoperiod ($F_{1,157} = 16.93$; $P < 0.01$)]. Thus, in the presence of *Bythotrephes*, *Daphnia* displayed a diel vertical migration, but not in the predator's absence (Fig. 1). The percentage of individuals in the upper 5-cm section of the cylinder was also significantly lower for *Daphnia* in the *Bythotrephes* water than for those in the control water ($F_{1,157} = 37.50$, $P < 0.01$), with no significant difference between day and night ($F_{1,157} = 1.97$, $P = 0.16$). Furthermore, the percentage of individuals in the lowest 5-cm section of the cylinder was

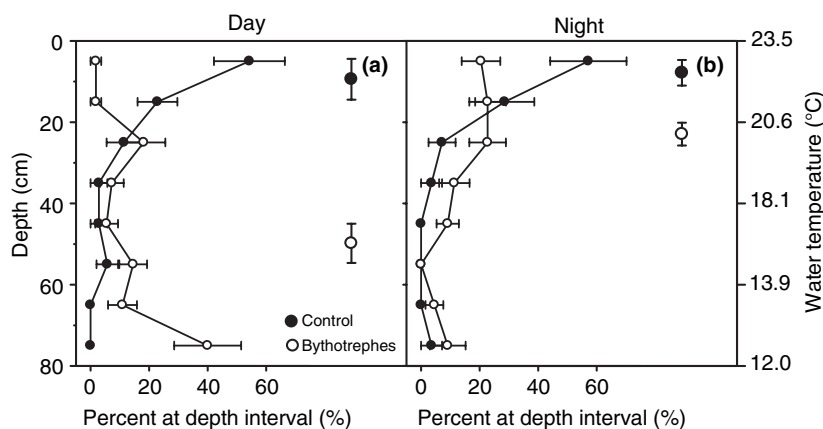


Fig. 1 Results of experiment 1. Day (a) and night (b) vertical position, plotted as a function of depth (left-hand axis) and temperature (right-hand axis), of *Daphnia mendotae* exposed to aged lake water without [solid circles (●)] and with [open circles (○)] *Bythotrephes* kairomone. The left-hand frequency distributions represent the mean percentage (\pm SE bars) of *Daphnia* at each depth interval (points have been positioned on the y-axis at the midpoint of their respective depth interval). Mean percentages for the top two 5-cm intervals have been combined, as have those for the bottom two 5-cm intervals. The right-hand points represent the mean depth (\pm SE bars).

significantly greater for the *Daphnia* in the *Bythotrephes* water than for those in the control water during the day, but not at night, leading to a significant interaction ($F_{1,157} = 5.20$, $P = 0.02$).

Bythotrephes kairomones also affected *Daphnia* growth. Over the duration of the experiment, the mean weight gained by *Daphnia* in the *Bythotrephes* water ($1.2 \pm 0.2 \mu\text{g}$) was less than one half that in the control water ($2.7 \pm 0.2 \mu\text{g}$, $F_{1,18} = 22.34$; $P < 0.01$). *Daphnia* mean specific growth rate in *Bythotrephes* water, $29.5 \pm 3.3\% \text{ day}^{-1}$, was 36% lower than in the control water, $45.7 \pm 1.8\% \text{ day}^{-1}$ ($F_{1,18} = 13.02$; $P < 0.01$).

In experiment 2, *D. mendotae* responded similarly to a gradient of *Bythotrephes* kairomone concentration in both water collected directly from the lake and prepared in the laboratory. Mean depth of *Daphnia* differed significantly among treatments ($F_{3,27} = 45.32$; $P < 0.01$), so pairwise comparisons were made between treatments (denoted significant below if P -value was < 0.05). Relative to the control, mean depth was not significantly different for *Daphnia* in lake water not inhabited by *Bythotrephes*, but was significantly deeper for *Daphnia* in lake water inhabited by *Bythotrephes* (Fig. 2a). Similarly, the vertical position of *Daphnia* was significantly deeper as *Bythotrephes* kairomone concentration increased in laboratory-prepared treatments. The behaviour of *Daphnia* in lake water not inhabited by *Bythotrephes* closely resembled those in control water, whereas the behaviour of *Daphnia* in lake water inhabited by *Bythotrephes* was similar to that in water with *Bythotrephes* kairomones that had been prepared in the laboratory (Fig. 2a). Significant differences were also found among treatment in the percentage of individuals in the extreme sections of the cylinder (Fig. 2b,c). Pairwise comparisons between treatments indicated that *Daphnia* in lake water not inhabited by *Bythotrephes* and in control water were found more frequently in the upper 5-cm section than *Daphnia* in water from *Bythotrephes* kairomone treatments ($F_{3,27} = 12.50$; $P < 0.01$). Furthermore, a significantly greater percentage of *Daphnia* were observed in the lower 5-cm extreme of the cylinder in water from *Bythotrephes* kairomone treatments than those in lake water not inhabited by *Bythotrephes* and control water ($F_{3,27} = 11.32$; $P < 0.01$).

Discussion

Our results support the hypothesis that the presence of *Bythotrephes* induces a behavioural response by

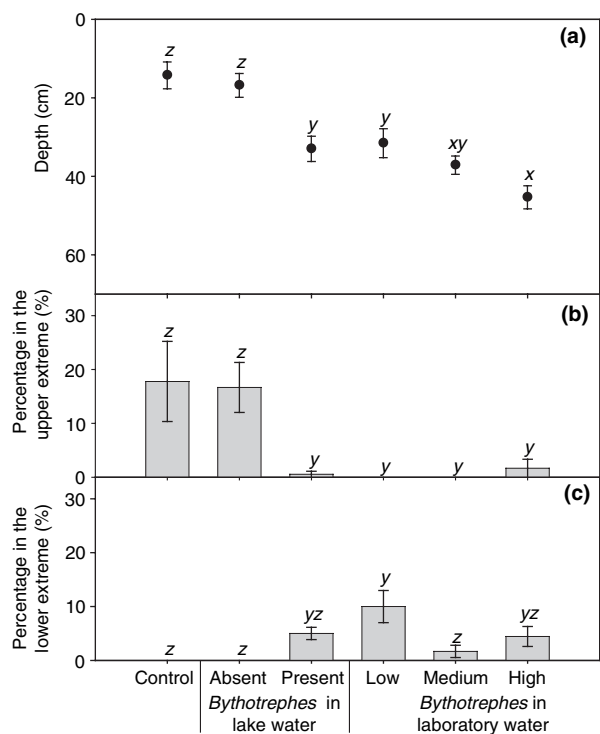


Fig. 2 Mean depth (a) and the percentage of *Daphnia mendotae* in the upper and lower 5-cm extremes (b and c, respectively) in experiment 2. Treatments included: control water; lake water not inhabited by *Bythotrephes*; lake water inhabited by *Bythotrephes* (approximately $0.010 \text{ Bythotrephes L}^{-1}$); low *Bythotrephes*-density laboratory-prepared water ($0.05 \text{ Bythotrephes L}^{-1}$); medium *Bythotrephes*-density laboratory-prepared water ($0.5 \text{ Bythotrephes L}^{-1}$); and high *Bythotrephes*-density laboratory-prepared water ($5 \text{ Bythotrephes L}^{-1}$). Values reported are treatment means ($\pm \text{SE}$). Means with different lowercase letters were significantly different as determined by ANOVA and Tukey's HSD tests ($P < 0.05$).

Daphnia. In both laboratory experiments, *Daphnia* exposed to *Bythotrephes* kairomones during the day were found in lower, cooler regions of the experimental columns, while *Daphnia* exposed to water with no kairomones inhabited upper, warmer regions. The difference between treatments lessened in magnitude when light intensity decreased, as seen in experiment 1, in which *Daphnia* exposed to *Bythotrephes* kairomones migrated upwards during the night, while the vertical distribution of *Daphnia* in the control treatment remained unchanged. Experiment 2 showed that *Daphnia* responded to lake water inhabited by *Bythotrephes*, but not without, suggesting that the concentration of kairomones in the field is sufficient to illicit a behavioural response by *Daphnia*.

The alternating day–night movement of *Daphnia* observed in our study (i.e. diel vertical migration), normally associated with a response to vertebrate planktivores (Stich & Lampert, 1981; Gliwicz, 1986; Loose & Dawidowicz, 1994; DeMeester *et al.*, 1998) could optimise the fitness of *Daphnia* facing a predation risk from *Bythotrephes*. *Bythotrephes*, unlike many aquatic invertebrate planktivores (Riessen *et al.*, 1988; Roche, 1990), uses visual cues to detect prey and may be five times more effective as a predator in the photic zone of the water column than in the aphotic zone (Muirhead & Sprules, 2003). Subsequently, inhabiting deeper, darker regions of the water column during the day would greatly reduce predation risk for *Daphnia*. At night, *Daphnia* can increase growth and developmental rates by migrating upwards into warmer near-surface regions when the risk from *Bythotrephes* is lower.

Our results are consistent with changes in *Daphnia* vertical distribution observed in pelagic systems invaded by *Bythotrephes*. For example, in Lake Michigan, a downward shift of *D. mendotae* in the water column corresponded with the invasion of *Bythotrephes* (Lehman & Caceres, 1993), and there is a strong positive relationship between the percentage of *D. mendotae* in the hypolimnion and *Bythotrephes* abundance that occurs seasonally in Lake Michigan (K.L. Pangle, unpublished data). In Harp Lake, Ontario, *D. mendotae* maintained a deeper vertical distribution than that of *Bythotrephes* during the day, but overlapped with the predator at night (Dumitru, Sprules & Yan, 2001; Muirhead & Sprules, 2003). In each case, the vertical migration induced by *Bythotrephes* could be responsible for the vertical distribution observed in the field. Note, however, that there are a number of possible alternative mechanisms for the observed field patterns (listed in the Introduction), and therefore this laboratory study makes clear the potential contribution of the behavioural response.

We predicted that predator-induced diel vertical migration would be associated with a cost, as is general to anti-predator tactics (reviewed in Harvell, 1990; Lima, 1998). In experiment 1, the vertical migration of *Daphnia* to *Bythotrephes* kairomone led to a 36% reduction in somatic growth. This reduction could have been caused by several mechanisms including inhabiting cooler water (Loose & Dawidowicz, 1994) and allocating more energy to early reproduction and morphological defences relative to

somatic growth (Tollrian, 1995). We evaluated how these possibilities contributed to the non-lethal effects on *Daphnia* in experiment 1. We calculated a predicted specific growth rate (SGR) for each individual (given their thermal experience during the experiment) using the equation: $SGR = -0.0009 T^2 + 0.0476 T - 0.1882$, where T is water temperature (°C). This equation was derived by fitting a non-linear model to published data (Hall, 1964) that reported *D. mendotae* growth rate over a wide range of temperatures (11–25 °C). The predicted reduction in *Daphnia* growth in the *Bythotrephes* treatment was close to the actual reduction (Fig. 3). This suggests that migratory behaviour into cooler water, and not modifications to morphology and life-history, were principally responsible for the non-lethal effect on growth rate.

For *Daphnia* species, somatic growth can be used as an approximation of fitness, as it is known to correlate strongly with population growth rate (Lampert & Trubetskova, 1996); thus, our results show a means by which *Bythotrephes* affects prey populations other than by direct consumption (i.e. non-lethal effect). These so-called non-lethal effects are predicted theoretically to play a critical role in predator-prey interactions (Abrams, 1982; Ives & Dobson, 1987; Abrams, 1993). Indeed, using simple models, Peacor & Werner (2004) showed that predator-induced reductions in growth rates on the order observed here (36%) are large enough to contribute substantially to the net effect of

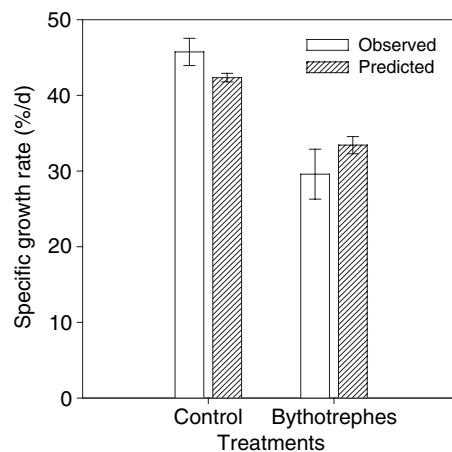


Fig. 3 Observed (open bars) and predicted (using a growth model, hatched bars) specific growth rate of *Daphnia mendotae* in experiment 1 exposed to aged lake water without and with *Bythotrephes* kairomone. Values reported are treatment means (\pm SE).

the predator on prey fitness. Empirical studies performed in mesocosms have also shown that the magnitude of non-lethal effects on prey population growth rates can be as large as or larger than that of lethal effects (Nelson, Matthews & Rosenheim, 2004; Boeing, Wissel & Ramcharan, 2005). Note that, in addition, such non-lethal effects may extend indirectly to affect prey food resources and competitors (reviewed in Abrams, 1995; Bolker *et al.*, 2003; Werner & Peacor, 2003; Schmitz *et al.*, 2004) via trait-mediated indirect interactions, further contributing to the net predator-prey interaction. These results, combined with our study, suggest that the induction of diel vertical migration may be as important to *Daphnia* population dynamics as changes caused by the direct consumption of *Daphnia* by *Bythotrephes*.

In conclusion, this study demonstrated the behavioural response of *D. mendotae* to *Bythotrephes* and a consequent non-lethal effect on growth. Our findings may be applicable to other systems, as *Bythotrephes* density used in the experiments were not only typical of Lake Michigan (Pothoven, Fahnenstiel & Vanderploeg, 2003), but also of those observed in Lakes Erie and Huron (Barbiero & Tuchman, 2004), smaller Canadian inland lakes (Boudreau & Yan, 2003), and lakes in the native range of *Bythotrephes* (Manca, Ramoni & Comoli, 2000; Palmer, Stich & Maier, 2001). Moreover, our study emphasises the complex nature of the impact of invasive species as well as provides an avenue for research into better understanding Lake Michigan food web dynamics. What is the relative magnitude of non-lethal effects compared to lethal effects and how are they transmitted through the food web via trait-mediated indirect interactions? Further, how do non-lethal effects occur under such short-term co-evolutionary periods? Addressing these questions could shed light into both the ecology and evolution of invasive species.

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